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THE COMPARATIVE MORPHOLOGY OF THE INSECT OVIPOSITOR

By G. G. E. Scudder

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With 10 Text-figures.

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I. Introduction

This paper considers the insect ovipositor, its structure and homologies. The most important comparative studies of the anatomy and morphology of the genital segments of the insect orders are by Crampton (1917, 1929) and Snodgrass (1933).

Snodgrass (1933) based his interpretations of the ovipositor of the higher insect orders on the condition in Machilidae, but elsewhere (Scudder 1957*a*, 1957*c*, 1961) I have stated that the Lepismidae provide a more satisfactory basic type. This concept is further developed in the following pages with due reference to fundamental homologies, established elsewhere (Scudder, 1961). The descriptions contained herein are presented in the hope that they will provide a basic comparative reference work for taxonomists and for further morphological work.

II. Terminology of the Basic Type of Ovipositor

It is possible to standardise the nomenclature of the parts of the ovipositor in all orders possessing genitalia developed on abdominal segments VIII and IX. A terminology which signifies in most cases the morphological homology of the various parts is used in preference to an artificial scheme. The artificial terminology of Snodgrass (1933) and others is therefore abandoned and that first used by Grassi (1887) is used as the basis for this new scheme.

Some synonyms of the terms used are given, but a more comprehensive list is given in Tuxen (1956); abbreviations refer to figures 1 and 2.

First gonocoxa (1 Gx)—the coxa of abdominal segment VIII (first genital).
Synonym : *First valvifer* (in some orders only).

First gonapophysis (1 Gpo)—the median process of abdominal segment VIII (first genital), possibly homologous with the eversible sac of a pregenital segment.
Synonyms : *First valvula*
Ventral valve or gonapophysis
Anterior valve or gonapophysis

Second gonocoxa (2 Gx)—the coxa of abdominal segment IX (second genital).
Synonym : *Second valvifer.*

Second gonapophysis (2 Gpo)—the median process of abdominal segment IX (second genital), possibly homologous with the eversible sac of a pregenital segment.
Synonyms : *Second valvula*
Inner valve or *gonapophysis*
Intermediate valve or *gonapophysis*
Median valve or *gonapophysis*

Gonangulum (Ga)—the sclerite attached ventrally to the base of the first gonapophysis and dorsally articulating with the second gonocoxa and tergum IX. Probably homologous with the antero-dorsal corner of the primitive coxa of segment IX.
Synonyms : *Anterior plate* (Snodgrass, 1935)
Triangular plate (Snodgrass, 1925, 1956)
Sclerites m + n (Snodgrass, 1933)
Valvifer (in some orders only)

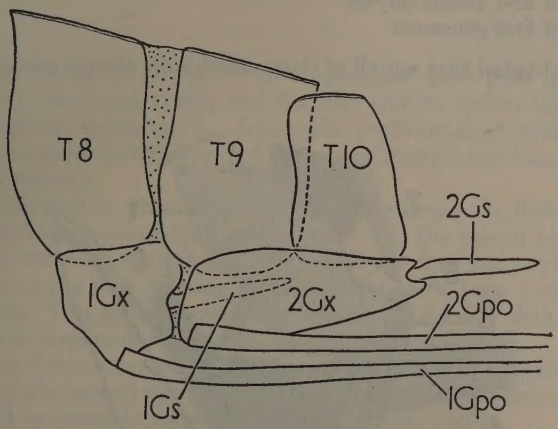
Gonoplac (Gpl)—the posterior outgrowth of the coxa of abdominal segment IX (second genital), forming part of, or a sheath for, the ovipositor in some orders. This may or may not be separated off as a separate sclerite.
Synonyms : *Third valvula* or *gonapophysis*
Dorsal valve
Lateral valve
Gonostyle (Michener, 1944*a*)

Gonostyle (1 Gs, 2 Gs)—the stylus of a genital segment.

Two new terms are introduced in the above scheme, namely, the gonangulum and the gonoplac. The true homology of the gonangulum has only recently been demonstrated (Scudder, 1961), and previously it has been variously interpreted in the different orders. Snodgrass (1935) rightly considered that in the Thysanura it was part of the second gonocoxa. In some other orders he considered it to be partly composed of a process of tergum IX and in others he homologised it with the first gonocoxa. In all the orders so far investigated in detail, it has been shown that this sclerite develops within the precincts of abdominal segment IX and is homologous with the antero-dorsal corner of the second gonocoxa, at least in the Lepismidae (Scudder, 1961). I have not used the term " triangular sclerite " as in many orders it is not triangular in shape.

The term gonoplac has been introduced for the posterior process of the second gonocoxa, mesad of the gonostyle, which appears to be homologous with the gonocoxal process present in some Thysanura (e.g. *Acrotelsella producta* (Esch.) figured by Womersley (1939 : 34)). This structure has previously been termed the third valvula or ovipositor sheath. In some orders (Hymenoptera) it does act as an ovipositor sheath, but in others (Orthoptera) it forms part of the ovipositor and does not act as a sheath. Since it has been shown that the first and second gonapophyses are probably not new outgrowths, but the modified eversible sacs of the genital segments, and that they are not homologous with the gonoplacs, the term third gonapophysis is unacceptable. Michener (1944*a*) has suggested the term " gonostyle " for this structure and this

term is being used in the Hymenoptera together with stylus, ovipositor sheath and third valvula. There have been a number of ontogenetical studies which have demonstrated that the gonoplacs arise as outgrowths of the second gonocoxae and are thus not homologous with the second gonostyles (Rawat, 1939 ; d'Rozario, 1942 ; Snodgrass, 1933). Further, the female larvae of *Blatta* and *Periplaneta* (Dictyoptera)



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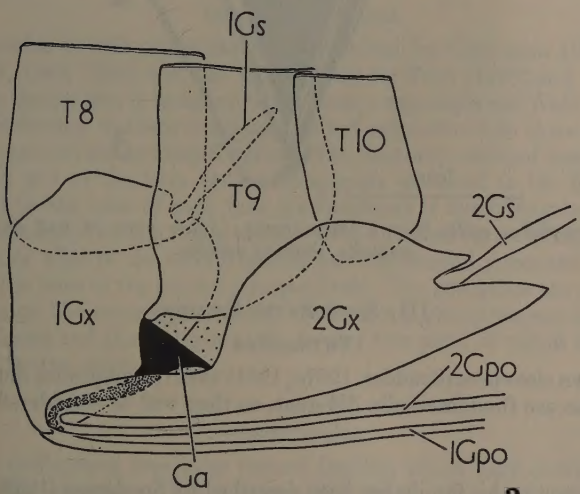

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FIGS. 1–2.—Inner view of skeletal parts of genital segments of: (1) *Petrobius maritimus* (Leach) (Thysanura); (2) *Lepisma saccharina* L. (Thysanura).

bear styli on the second gonocoxae and these are present together with the rudiments of the gonoplacs in later instars, although they are lost in the adult (Walker, 1919 ; Snodgrass, 1933 ; Quadri, 1938, 1940 ; Gupta, 1950 ; *personal observation*). The term gonostyle, which indicates the stylus of a genital segment, is therefore wholly unacceptable for the structure in question. Further, the terms styloid, proposed by Verhoeff (1893) and gonostyloid, used by Stys (1959), are too similar to gonostyle for convenient use.

It has been found that certain muscles of the ovipositor (fig. 3, 1–4) act as " landmarks " for interpretation of the insect ovipositor ; these may be enumerated as follows :

1. extensor of gonapophyses
2. retractor of second gonapophyses
3. retractor of first gonapophyses
4. retractor of first gonocoxa

It should be emphasised that not all of these muscles are always present in all orders (Scudder, 1959).

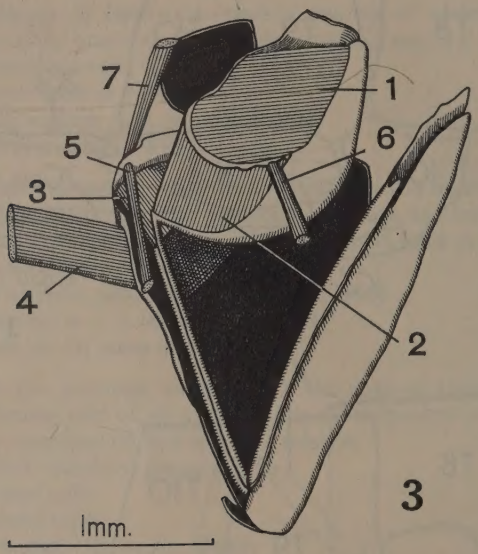


FIG. 3.—*Dicranocephalus agilis* (Scop.) (Hemiptera) : inner view of half section of female genitalia, showing muscles.

III. SYSTEMATIC REVIEW

THYSANURA

I have shown elsewhere (Scudder, 1957*a*, 1961) that the ovipositor in the Machilidae and Lepismidae are fundamentally different, so they will be considered apart.

Machilidae

The ovipositor in this family has been described by Snodgrass (1933), Maki (1938), Matsuda (1957), Grassi (1887), Bär (1912) and Scudder (1957*a*, 1957*c*, 1961). The ovipositor of *Petrobius maritimus* (Leach) has been studied and the brief description below refers to this species.

The two genital segments, abdominal segments VIII and IX (fig. 1), are almost exactly alike. Segment VIII carries ventrally the first gonocoxae, which posteriorly bear the first gonostyles and ventrally carry the first gonapophyses. Similarly, segment IX carries the second gonocoxae, second gonostyles and second gonapophyses. The gonocoxae are homologous with the coxae of the pregenital segments and the gonostyles are likewise homologous with abdominal styli ; they are apparently not homologous with the styli born on thoracic legs (Woodland, 1952). The homology of the gonapophyses has been much discussed, and the literature reviewed by Gustafson (1950), Mat-

suda (1957) and Stys (1959). They have been considered of sternal origin by Heymons (1896*a*, 1896*b*, etc.) and Matsuda (1957), homologous with the thoracic legs by Verhoeff (1893) and coxal endites by Snodgrass (1933, 1935), whilst Silvestri (1905), Gupta (1950), Gustafson (1950) and Stys (1959) consider them homologous with the eversible sacs of pregenital segments. As stated elsewhere (Scudder, 1957*c*), on the evidence available, the latter seems most plausible.

Lepismidae

Descriptions of the ovipositor of the Lepismidae have been given by Lacaze-Duthiers (1853), Snodgrass (1935) and Scudder (1957*a*, 1957*c*, 1961). The female genitalia of *Lepisma saccharina* L., *Lepismodes* (=*Thermobia*) *domesticus* (Packard) and *Ctenolepisma quadriseriata* Packard have been studied and found to be identical in all essential respects.

As in the Machilidae, abdominal segment VIII carries the first gonocoxae, first gonostyles and first gonapophyses, and segment IX, the second gonocoxae, second gonostyles and second gonapophyses. However, the first gonapophysis, as well as being attached to the first gonocoxa, has attached to its base a triangular sclerite, the gonangulum. This sclerite posteriorly articulates dorsally with tergum IX and ventrally with an apparent notch in the second gonocoxa.

The drawing of the ovipositor by Snodgrass (1935, fig. *G*, p. 610) show the gonangulum attached to the second gonapophysis instead of the first gonapophysis as shown in figure 2, and as correctly shown by Lacaze-Duthiers (1853).

Grylloblattodea

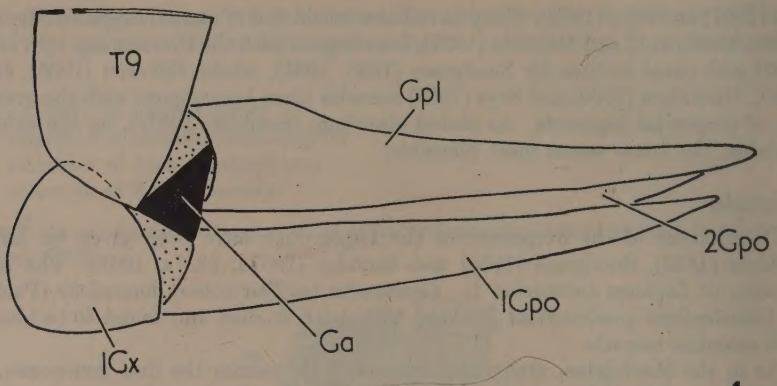
The ovipositor in this order has been described by Crampton (1927, 1929) and Walker (1919, 1943, 1956) and the musculature by Ford (1923) and Walker (1943). The following description is based on *Grylloblatta campodeiformis* Walk.

In *Grylloblatta* (fig. 4) there is a long exserted ovipositor with three well developed pairs of subequal lanceolate shaped valves. The ventrally situated first gonapophyses are sclerotized and at the base are membranously attached to the first gonocoxae. Also attached to the base of each first gonapophysis is the triangular gonangulum. This attaches dorsally, as one would expect, to the ventral corner of the ninth tergum and the anterior edge of the second gonocoxa. The second gonocoxa appears as an expansion at the base of the second gonapophysis. The gonoplacs are well sclerotized and are borne on the second gonocoxae. The second gonapophyses lie between the first gonapophyses and the gonoplacs, the former two pairs of valves interlocking by a tongue and groove mechanism.

Orthoptera

The order Orthoptera comprises several families which vary considerably in the condition of the ovipositor. The Tettigoniidae retain the second gonapophyses as well developed structures, as shown by Snodgrass (1933) (in *Scudderia*) and by many other authors. The Gryllidae have the second gonapophyses reduced to membranous flaps, but in all other respects show the same general structure of the order. The ovipositor of *Acheta* (=*Gryllus*) *domesticus* (L.) is here discussed as an example. The remarks below were confirmed by a study of the Tettigonid *Leptophyes punctatissima* (Bosc.).

The ovipositor of the Gryllidae has been described by Walker (1919), Chopard (1920), Crampton (1917, 1929), Snodgrass (1933), Spann (1934) and Gupta (1950). The musculature has been considered by DuPorte (1920), Ford (1923) and Snodgrass (1933), and many of the authors mentioned above have described the post-embryonic development of the ovipositor.



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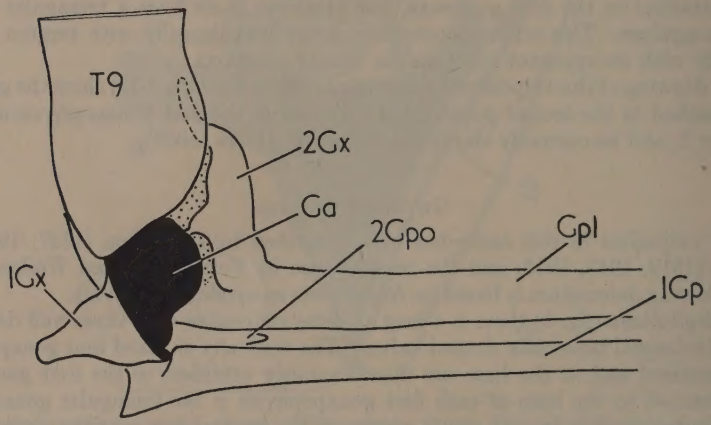

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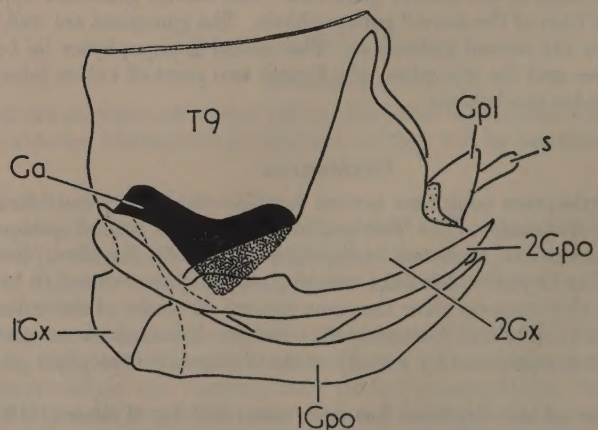

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FIGS. 4–6.—(4)–(5). External view of left side of female genitalia of: (4) *Grylloblatta campodeiformis* Walk. (Grylloblattodea) (after Walker, 1943, 1956); (5) *Acheta domesticus* (L.) (Orthoptera). (6) Internal view of right side of female genitalia of *Aeshna grandis* (L.) (Odonata).

In the ovipositor of the adult *Acheta* (fig. 5), only two pairs of valves are elongate and sclerotized. The gonoplacs are ridged ventrally and interlock in the groove on the dorsal surface of the first gonapophyses. This is in marked contrast with the condition in almost all the other orders where it is the first and second gonapophyses alone that are the interlocking structures forming the shaft of the ovipositor.

Attached to the base of the first gonapophysis is an irregularly triangular sclerite which is the fused first gonocoxa and gonoplac. This composite sclerite has an anteriorly projecting apodeme for muscle attachment arising from the first gonocoxal part and posteriorly has two articulations on the gonangulum portion. Dorsally there is a condyle which articulates with the antero-ventral corner of the ninth tergum and posteriorly is located a notch which articulates with a condyle on the anterior part of the second gonocoxa. The latter is rather an elongate sclerite, which ventrally bears the membranous flap-like second gonapophysis and dorsally is continuous with the valvular gonoplac.

I have homologised the anterior or ventral valve of the Orthoptera with the first gonapophysis of the Thysanura. This is contrary to the opinion of Qadri (1940) who states " It may definitely be stated that the anterior valves of Gryllidae cannot be compared with the gonapophyses of the eighth segment of Thysanura ". He continues, in talking about the anterior valves " that they represent the drawn-out or modified coxites of the eighth segment corresponding to the lateral valves, does not hold good, since the anterior valves become clearly differentiated from the coxites of the eighth segment by a distinct joint quite early during development ". Gupta (1950) regarded the first gonapophysis as an outgrowth of the coxa and hence serially homologous with the gonoplac. Qadri's view is based on the theory that the gonapophyses are outgrowths of the gonocoxae, a view supported by several previous authors. Silvestri (1905), Gupta (1950), Gustafson (1950), Scudder (1957*c*) and Stys (1959) have stated, however, that the gonapophyses (second gonapophyses in the case of Gupta) are more plausibly homologised with the eversible sacs of the pregenital segments in the Thysanura, and Gustafson states " The primary gonapophyses, as possessed by the Thysanura, are structures distinct from the coxites ... ". I have also concluded that primarily there was no sclerotised connection between the first gonapophysis and the first gonocoxa, only a membranous connection. Thus the assumption, which led Qadri to come to the conclusion that the first gonapophyses are probably homologous with the styli of the coxites of the eighth segment of the Thysanura, appears incorrect. He further states that the first gonapophyses may be regarded as homologous structures amongst all the families of the Orthoptera if their original mode of development is represented by the condition found in the Gryllidae. Here rudiments of the first gonapophyses develop far from the mid-line and are dragged inwards by the development of the spermathecal invagination. In the Blattidae and Acrididae, the spermathecal invagination takes place before the formation of the rudiments of the first gonapophyses; when the latter do arise, they are located near the mid-line. Other studies have shown that structures can be retarded or accelerated in development in different groups (*see* Berrill, 1945; de Beer, 1951; and Dalcq, 1957) and thus I am inclined to regard the differences in development in time of the first gonapophyses in the different families of Orthoptera as not inconsistent with the view that they are homologous throughout this order: d'Rozario (1942) has shown that similar acceleration or retardation phenomena occur in the development of the genitalia in the Hymenoptera.

I have discussed the development of the ovipositor elsewhere (Scudder, 1961) and described the fusion of the first gonocoxa with the gonangulum.

Dictyoptera

The ovipositor in the Dictyoptera has been described by Miall and Denny (1886), Peytoureau (1893), Bordas (1909), Walker (1919), Vogel (1925), Crampton (1925,

1929), Nel (1930), Snodgrass (1933, 1952), Qadri (1938, 1940), and Gupta (1950); Ford (1923) and Gupta (1950) have described the musculature. I have dissected *Blatta orientalis* (L.), *Periplaneta americana* (L.), *Blaberus discoidalis* A–S. (Blattaria) and *Mantis religiosa* (L.) (Mantodea); the first mentioned is considered here.

In *Blatta* the ovipositor is not exserted, but is contained in the vestibulum, a cavity formed by the enlarged seventh sternum. The presence of a vestibulum has necessitated the ovipositor in this group being considerably modified. However, it is possible to trace all of the component parts.

The ovipositor is composed of three pairs of valves, the first and second gonapophyses and the gonoplacs, which are subequal in length. Attached to the base of the first gonapophysis is a rather flat sclerite which represents the fused first gonocoxa and gonangulum. This is located in the roof of the vestibulum and is connected with the ninth tergum by a narrow sclerotised band. Also, this composite sclerite is connected to a lobe of the second gonocoxa, but this is not always easy to observe because this region is rather weakly sclerotised. The second gonapophysis and the gonoplac both arise from an enlarged common basal part which represents the second gonocoxa.

Snodgrass (1952) states that the study of Ford (1923) suggests that the sclerites in the floor of the vestibulum represent the eighth abdominal sternum or first gonocoxa, but Gupta (1950) believes that those in the roof of the vestibulum are derived from the eighth sternum. The drawing by Snodgrass (1933 : 74) of *Blatta orientalis*, shows the first gonocoxa (=first valvifer) fused to the base of the first gonapophysis (=first valvula), but the drawing of *Periplaneta* by the same author (1952 : 331) omits this sclerite. Certain aspects of the musculature, as suggested by Snodgrass (1933), suggest that the earlier drawing (1933) represents the probable condition to be expected in the group. The gonangulum has previously been interpreted as the " valvifer " by Gupta (1950) and the ventral part of the ninth tergum by Snodgrass (1933). The latter author labels the gonangulum " *e* " and states that it has a connection " *g* " with tergum IX and is attached to the second gonocoxa and the first gonapophysis. The second gonocoxa was called the " basal plate of the second and third valvulae " and labelled " *e* " by Snodgrass (1952).

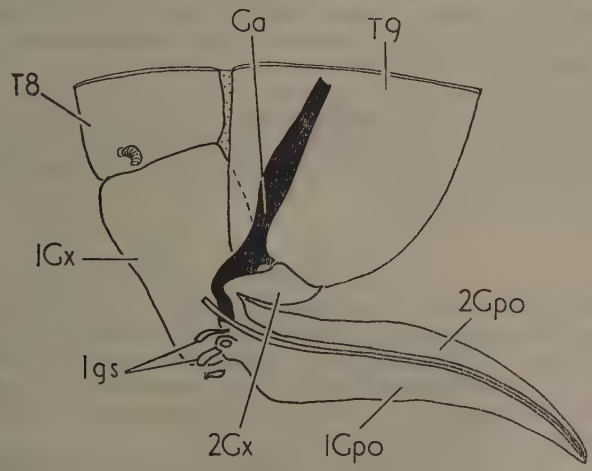
Odonata

A well developed ovipositor is present in all known Zygoptera and Anisozygoptera and in many Anisoptera (*e.g.* Aeshnidae and Petaluridae). The structure of the female genitalia of the Odonata has been described by Van der Weele (1906), Tillyard (1917), Walker (1919), Machotin (1929), Crampton (1929), Chao (1953), Asahina (1954) and Fraser (1956). The ovipositor of *Aeshna grandis* (L.) (fig. 6) is described here as an example.

The first gonocoxae are seen situated ventral to the ninth tergum. The heavily sclerotised first gonapophysis is gently curved dorsally towards the apex and the rather truncate base is attached to the first gonocoxa. Also attached to the first gonocoxa is a large triangular sclerite, the gonangulum, which can sometimes be seen projecting slightly beneath the ninth tergum when viewed from the exterior. The gonangulum has the usual connections with the ninth tergum and second gonocoxa. The second gonapophysis is very similar to the first gonapophysis in shape, but more slender. It is attached basally to the second gonocoxa, which is a large quadrate sclerite situated ventro-posteriorly. In *Aeshna* the second gonocoxa bears posteriorly two sclerites which are membranously connected to it. One of these, a small triangular shaped sclerite, may represent the gonoplac. The other stylus-like structure would appear at first sight to be the second gonostyle. However, such stylus-like structures are also seen in some Hymenoptera and may be secondary structures and not true gonostyles.

Thysanoptera

Melis (1933) has figured the ovipositor of *Melanthrips* and these drawings were adopted by Pesson (1951). More recently, Jones (1954) has described the ovipositor of *Chirothrips hamatus* (Trybom).



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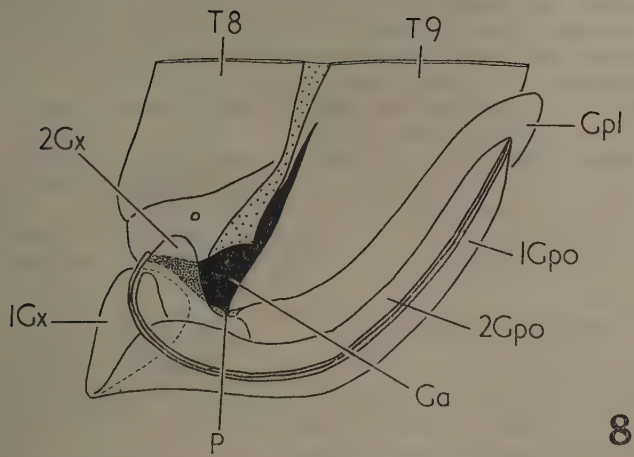

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Figs. 7–8.—Internal view of right side of female genitalia of: (7) *Thrips validus* Uzel (Thysanoptera); (8) *Tettigella viridis* (L.) (Hemiptera).

A true ovipositor is present in most of the suborder Terebrantia, but is absent in the Tubulifera. I have examined many species of thrips and *Thrips validus* Uzel (G. D. Morison *det.*) is considered here.

In *T. validus* (fig. 7) the first gonapophysis is well developed and sclerotised. Basally it is attached to the first gonocoxa, the latter being a sclerite which is closely associated with the eighth tergum dorsally. The first gonapophysis is also connected to the ninth tergum by a thick sclerotic rod. This rod postero-ventrally also articulates with the second gonocoxa. It represents the gonangulum, which is very elongate and

has fused with the ninth tergum. Such a fusion of the gonangulum with the ninth tergum has been observed in the Psocoptera (Scudder, *unpubl.*) and is here reported in the Hemiptera (*see below*).

The second gonocoxa is a small triangular sclerite which is continuous ventrally with the elongate second gonapophysis. The second gonapophysis, which is sclerotised, is ridged ventrally and fits into a groove on the dorsal side of the first gonapophysis.

I have found no trace of the gonoplacs and this is in agreement with the findings of Jordan (1888) and Jones (1954).

Small inter-gonocoxal sclerites present in the membrane at the base of the first gonapophyses do not form part of the ovipositor complex.

The first gonocoxa was interpreted as the eighth sternum by Jones (1954); he further called the gonangulum the " ninth apodeme ". Melis (1933) did not recognise the gonangulum in his drawings.

Hemiptera

The most important works to date on the ovipositor in the Heteroptera are those of Bonhag and Wick (1953), Davis (1955, 1956, 1957), Galliard (1935), Guthrie (1954), Kullenberg (1946, 1947), Larsen (1938), Ludwig (1926) and Scudder (1957*b*, 1959), which deal with the sclerotised parts and the musculature. Snodgrass (1933) and Müller (1942) have described the ovipositor in various Auchenorrhyncha and Kramer (1950) considered five families in detail.

The structure of the ovipositor in *Tettigella viridis* (L.) (Cicadellidae) is illustrated (fig. 8). There is little difference between the ovipositor of the Auchenorrhynchous Homoptera and Heteroptera.

The ventro-lateral part of tergum VIII in the Hemiptera is often represented as a separate sclerite, the paratergite, which carries spiracle VIII. The first and second gonocoxae are quite different in shape and size, the second gonocoxae being smaller and more slender than the first. In the cimicomorph section of the Heteroptera there is a marked tendency for the first gonocoxae to fuse dorsally with the eighth paratergite; the second gonocoxae may fuse together posteriorly in some families of Heteroptera (*e.g.* Pyrrhocoridae) (Scudder, 1959).

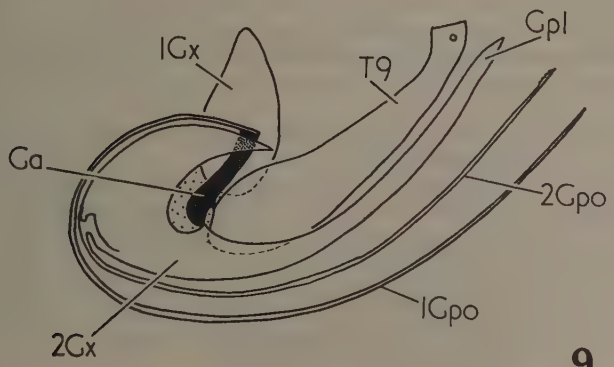
Both the first and second gonapophyses are present and usually laciniate in shape. The whole length of the dorsal edge of the first gonapophysis is heavily sclerotized and forms the grooved first ramus. Similarly, the whole length of the ventral edge of the second gonapophysis is heavily sclerotized and forms the interlocking ridged second ramus. In the Hemiptera, the second gonapophyses are usually united dorsally along their length.

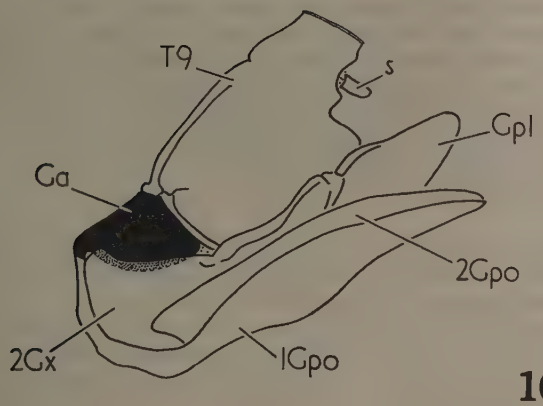
In the Hemiptera, the gonangulum is triangular or often an inverted V-shaped sclerite. The ventral part of the anterior limb or edge of the gonangulum attaches to the anterior end of the first ramus, which is often produced beyond the end of the first gonapophysis proper. The ventral end of the posterior limb of the gonangulum articulates with the second gonocoxa about the mid-point. This articulation (*p*) forms the fulcrum on which the second gonocoxa is rocked by opposing muscles attached to the anterior and posterior parts of the gonocoxa and originating on tergum IX; the point of articulation (*p*) is not part of tergum IX. The dorsal angle of the gonangulum, which in *Lepisma* articulates with tergum IX, in the Hemiptera is fused to tergum IX. This is the condition seen in the Tingidae (Scudder, 1959). Usually, however, as in *Tettigella*, the whole of the posterior side of the gonangulum is fused to the antero-ventral edge of tergum IX. A gonoplac is present, attached to the second gonocoxa; there is a tendency for the gonoplac to be reduced or absent in some Heteroptera.

A discussion of the interpretation of some structures in the hemipterous ovipositor has been given elsewhere (Scudder, 1959).

Hymenoptera

There have been numerous accounts of the structure of the ovipositor in the Hymenoptera, amongst which the study of Snodgrass (1933) is the most important; Domenichini (1953) figures and labels the ovipositor of a number of Chalcidoidea and Richards





Figs. 9–10.—Internal view of right side of female genitalia of: (9) *Tetramesa calamagrostidis* (Hed.) (Hymenoptera); (10) *Tenthredo maculata* Geoff. (Hymenoptera).

(1956) figures details of various families of Hymenoptera. The development of the ovipositor and sting has been investigated on several occasions and d'Rozario (1942) gives a review of the literature and an account of his own studies.

I have examined the ovipositor of members of the Xyelidae, Siricidae, Tenthredinidae (fig. 10), Ichneumonidae, Cynipidae, Eurytomidae (fig. 9), Scelionidae, Torymidae, Apidae, Formicidae and Vespidae, and find that all have the same basic structure.

The shaft or piercing part of the ovipositor is composed of two slender pairs of interlocking valves, the first and second gonapophyses, the latter pair being united along their whole length as in *Lepisma*. To the base of the first gonapophysis is

attached the gonangulum. This latter sclerite has the typical articulations with the ninth tergum and second gonocoxa, and whereas in Tenthredinidae (fig. 10) it is a triangular-shaped sclerite, in the Eurytomidae (fig. 9) it is rather strap-shaped.

In the majority of the Hymenoptera examined, no trace of the first gonocoxa could be found. However, in the Chalcidoidea, an oval shaped sclerite situated ventral to tergum VIII would appear to be homologous with the first gonocoxa.

The base of the second gonapophysis is attached to the broad and elongate second gonocoxa and from the posterior of the latter arises the gonoplac, the shape of which is very variable. A small stylus-like sclerite is present in *Tenthredo* (fig. 10) attached to the posterior of tergum IX, but this should not be homologised with the second gonostyle.

Snodgrass (1933) and Michener (1944*b*, 1956) state, incorrectly, that the hymenopterous ovipositor is peculiar in the Insecta.

I have been unable to find the first gonocoxa in the Hymenoptera examined (including *Xyela*), except perhaps in the Chalcidoidea, and assume that it has been lost in the remaining superfamilies; in the Chalcidoidea, there is usually an oval sclerite, ventral to tergum VIII. From the study of Domenichini (1953) this sclerite appears to be present in most families of Chalcidoidea. The latter author called it the "lamine dipendenti dall' VIII urosterna". Richards (1956) interprets it as a laterotergite; d'Rozario (1942) and Rakshpal (1946) did not include it in their studies on the Pteromalidae and Eulophidae respectively.

Laterotergites are known to occur commonly in the Hymenoptera. Richards (1956) gives the following examples: Chrysididae, segments 2–4; Scelionidae, 2–6; Platygasteridae, 3–7). He states that the spiracular openings lie at the sides of the terga. It appears that all these laterotergites carry the spiracles (if the latter are present); primitive *Xyela julii* (Breb.) (Xyelidae) has spiracles located in the laterotergites, as have the highly modified Cheloninae (Braconidae). It seems to be unusual to find a laterotergite without a spiracle when both structures are present on the same segment, as on segment VIII in Chalcidoidea. Neither Domenichini nor Richards could have considered the chalcidoid laterotergite on segment VIII as the first gonocoxa (=first valvifer), since they followed Snodgrass and interpreted the gonangulum as the first gonocoxa.

IV. The Ovipositor, Classification and Evolution

The ovipositor of *Petrobius* (Machilidae) is quite different from that of *Lepisma*, *Ctenolepisma* and *Lepismodes* (Lepismidae). This appears to be a fundamental difference between the two families. I consider that the condition in *Petrobius* probably represents the most primitive ovipositor in the Insecta, the Machilidae representing a separate offshoot of the main stem of the Insecta, a branch which arose before the evolution of the gonangulum in the ovipositor. Ross (1955), from a study of the abdominal appendages, the mouth parts and the tentorium, concluded that the Machilidae and Lepismidae represented separate offshoots, and regarded these two groups as separate orders, the Microcoryphia and Thysanura *sensu str.*, respectively. It is interesting to note that Börner (1904) erected two suborders, the Archaeognatha and Zygentoma, for the Machilidae and Lepismidae, respectively. The studies on the locomotion in the two groups (Manton, 1953) and the tracheal system (Stobbart, 1956) also seem to support these conclusions.

The structure of the ovipositor in the Odonata (where it exists) and in *Grylloblatta* is virtually identical with the archaic *Lepisma* type. That *Grylloblatta* has this structure and the Orthoptera and Dictyoptera, as far as examined, have a more highly modified ovipositor, is further evidence of the primitiveness of this insect.

In the other pterygote orders, various modifications of the *Lepisma* type are seen. In the Orthoptera and Dictyoptera, the first gonocoxa and gonangulum fuse to form a composite sclerite. In the hemipteroid orders (Hemiptera, Psocoptera, Thysan-

optera), the gonangulum has fused with tergum IX ; the fact that the three above mentioned hemipteroid orders have the same modification of the archaic type supports their position together as a natural group. The ovipositor of the Hemiptera, and the other hemipteroid orders, is not more generalised than that of the Hymenoptera or orthopteroid orders, as stated by Snodgrass (1933). Finally, in the Hymenoptera, the first gonocoxae appear to have been lost in evolution, except perhaps in the Chalcidoidea.

It is found that the main pterygote orders examined fall into a number of distinct groups on the characters of the ovipositor, and these groups coincide with the grouping obtained from the study of other structures ; the groups are listed in Table I. Each group has its own special modification of the archaic *Lepisma*-type of ovipositor. This shows that once the peculiarities had been evolved in the ovipositor of each group, another group is unlikely to have evolved from it. For instance, it is unlikely that the Hemiptera evolved from the Orthoptera, because in the latter the gonangulum has fused to the first gonocoxa, whereas it is fused to tergum IX in the former. Further, the Hymenoptera, with the free gonangulum, seem not to have evolved from either the Hemiptera or Orthoptera, or *vice versa*, because in both of these the gonangulum has fused with other sclerites and most Hymenoptera have lost the first gonocoxa.

V. Summary

Snodgrass (1933) based his interpretation of the ovipositor in the higher insect orders on the condition in the Machilidae. A more satisfactory interpretation is obtained if the structure in the Lepismidae is taken into account as an intermediate type from which the pterygote ovipositor was derived. *Lepisma* and the pterygote orders possess a triangular sclerite, here termed the gonangulum, in the ovipositor. This is absent in *Petrobius* and other Machilidae, and in the pterygote orders has been variously interpreted as the first gonocoxa, part of the second gonocoxa or an outgrowth of the ninth tergum and the first gonapophysis. A comparative study of the sclerites and development of the ovipositor in *Petrobius* and *Lepisma* shows that the gonangulum is homologous with the antero-dorsal corner of the limb base of the ninth segment (Scudder, 1961).

The term gonoplac is introduced to replace the term gonostyle as used by Michener (1944*a*, 1944*b*, 1956) for the third valvula of Snodgrass (1933) ; the terms styloid or gonostyloid as used by Verhoeff (1893) and Stys (1959) are considered too like gonostyle for convenient use.

The structure of the ovipositor in the Grylloblattodea, Orthoptera, Dictyoptera, Odonata, Thysanoptera, Psocoptera, Hemiptera and Hymenoptera is also described and discussed and it is shown that all can be derived from the archaic *Lepisma* type.

VI. Acknowledgments

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TABLE I.——*Grouping of insect orders suggested by a study of the ovipositor*

1. Ovipositor without gonangulum . . . . . MACHILIDAE
2. Ovipositor with gonangulum and without loss or fusion of sclerites
   LEPISMIDAE, GRYLLOBLATTODEA, ODONATA
3. Ovipositor with gonangulum and first gonocoxa fused . . ORTHOPTERA, DICTYOPTERA
4. Ovipositor with gonangulum and tergum IX fused (sometimes first gonocoxa and tergum VIII also fused) . . . . . HEMIPTERA, PSOCOPTERA, THYSANOPTERA
5. Ovipositor with free gonangulum and first gonocoxa very reduced or absent altogether
   HYMENOPTERA

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VIII. Key to Lettering of Figures

Ga, gonangulum
Gpl, gonoplac
1Gpo, *2Gpo*, first and second gonapophyses
1Gs, *2Gs*, first and second gonostyle
1Gx, *2Gx*, first and second gonocoxa
Igs, inter-gonocoxal sclerites
p, pivot
s, stylus-like sclerite
T8, *T9*, *T10*, terga VIII, IX and X
1, extensor muscle of gonapophyses
2, retractor muscle of second gonapophysis
3, retractor muscle of first gonapophysis
4, retractor muscle of first gonocoxa
5, anterior dilator muscle of genital chamber
6, posterior dilator muscle of genital chamber
7, tergal muscle of first gonocoxa